

Effect of Practice on Brain Activity: An Investigation in Top-Level Rifle Shooters

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ABSTRACT

DI RUSSO, F., S. PITZALIS, T. APRILE, and D. SPINELLI. Effect of Practice on Brain Activity: An Investigation in Top-Level Rifle Shooters. *Med. Sci. Sports Exerc.*, Vol. 37, No. 9, pp. 1586-93, 2005. **Purpose:** The study investigated the effect of motor experience on the brain activity associated with self-paced movement of the left and right index fingers. **Method:** Movement-related cortical potentials (MRCP) are indices of cortical activation related to movement preparation and execution. MRCP were recorded in two groups of subjects: high-level rifle shooters and control subjects without any shooting experience. All subjects were right-handed. Four MRCP components were considered: Bereitschaftspotential (BP), negative slope (NS'), motor potential (MP), and reafferent positivity (RAP). The BP and NS' components, which emerged before movement onset, were associated with preparation for voluntary movements. **Results:** Differences between groups were found in the amplitude and latency of these components for right finger flexion (but not for left finger flexion). BP and NS' latencies were longer for shooters than for controls; amplitudes were smaller. In contrast, no difference was found between groups for MP and RAP amplitude or latency. Source analysis, based on a realistic model of the brain, showed with high reliability (97% of variance explained) that the BP (time window: -1500 400 ms), NS' (-400 50 ms), MP (0 +100 ms) and RAP (+100 +200 ms) components were generated in the supplementary motor area, premotor area, primary motor area, and somatosensory area, respectively. No difference was found between groups regarding the localization of generators of all components. **Conclusion:** Results are discussed in terms of neural economy of motor preparation due to the specific practice involved in shooting. **Key Words:** MOVEMENT-RELATED CORTICAL POTENTIALS, READINESS POTENTIALS, ATHLETES, SOURCE ANALYSIS, MOTOR EXPERIENCE

Performance on a variety of motor tasks, for instance, skiing, dancing, and piano playing, improves through training; this points to the remarkable plasticity of the human brain to motor experience. Two main research lines investigate this phenomenon in humans. The first studies the structural changes that occur in the brain following motor experience. Motor training affects the extent of the cortical representation of the most used body segment. Depending on the temporal extent (amount) of motor practice, these changes can be reversible (26) or stable (11).

The other research line, relevant for the present study, investigates the effects of motor experience at the functional level with both functional magnetic resonance imaging (fMRI) and electrophysiological techniques. One interesting finding is

that past motor experience interacts with motor learning. Differences in the brain activity of expert and naïve subjects while they performed a motor task were documented in terms of (a) decreased cortical activation in the motor preparation phase preceding the actual movement, that is, larger percentage of alpha rhythm before movement in expert than in nonexpert subjects (5,14,18,19,31); (b) decreased cortical activation in the execution phase as a function of the training period, that is, the longer the training, the lower the activation (21); and (c) decrement of bilateral activation in favor of left or right hemispheric dominance (i.e., a more lateralized pattern of activation during highly practiced motor sequences) depending on both the motor skill and the degree of hemispheric control for that skill (3,17,24,27). Overall, these data suggest that an expert brain needs fewer resources than a nonexpert brain to prepare and execute a motor act. Further, practice suppresses cognitive processes irrelevant for the motor task: automatization increases and less cognitive effort is devoted to the motor task (18,19). Following motor practice, the task is performed in “economy,” with less cognitive effort and less (or more lateralized) activation of cortical areas devoted to motor activity (13).

The main goal of the present study was to define the level at which postulated “economy” takes place in terms of

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processing (preparation and/or execution), specific cortical areas, and hemispheric specialization. Previous electrophysiological studies have addressed this issue in an indirect way, deriving the concept of economy from variation of the global EEG activity. In contrast, in the present study we examined the specific indices of brain activity, as the event-related potentials (ERP) associated with motor preparation and execution (4,6,10,32). To achieve this goal, we selected one of the best methods for investigating cortical activity related to motion: movement related cortical potential (MRCP) recording. In contrast with fMRI, which has poor temporal resolution because it averages brain activity across minutes of recording, the electrophysiological technique of MRCP allows assessing the time course of brain events with precision (on the order of milliseconds). Moreover, with multielectrode techniques, it is possible to localize the sources of cortical activity with sufficient precision. Milestone studies in the 1960s defined the MRCP components associated with preparation for voluntary movements as Bereitschaftspotential (BP) and negative slope (NS') (6). After these components, the motor potential (MP) and the reafferent potential (RAP) are present. They are often called postmovement potentials (4) and are associated with movement execution. The latency and scalp topography of the MRCP components are known (32). However, their generators and their temporal order of activation have only been investigated in the past decade (8,32,33). The major sources of the BP and NS' components have been identified in the associative motor areas, that is, the supplementary motor area (SMA) and the premotor area (PMA); however, a contribution of subcortical structures cannot be excluded (28). Regarding the cortical activity associated with the execution phase, the generators reflected into the MP component were found in the primary motor cortex. After movement, the primary somatosensory area was active, as reflected by the RAP component (8,32,33).

Athletes constitute a particularly interesting population for investigating the effect of motor practice on the expert brain. In the present study, we considered top-class clay target shooters. These athletes are able to shoot one (or a couple of) small-sized targets coming up from a predictable (or unpredictable) portion of the field. The task is performed every day for hours with remarkable success. Clay-target shooting requires high-level visuomotor coordination, attention, and resilience to fatigue (1,9). In particular, these athletes show an advantage with respect to control subjects even when elementary visuomotor functions are tested, that is, their saccadic reaction time is reduced with respect to controls (9). An interpretation of this advantage was given in terms of shorter saccadic motor preparation after shooting training.

In the present study, we recorded MRCP in shooters using a typical paradigm, that is, the self-paced, alternating finger movement, which has proved useful in evaluating motor preparation and execution both in normal subjects (10) and in patients (8). To our knowledge, this paradigm has only been used once with athletes (20). In keeping with previous findings (9), we expected that key pressing, an action in-

volving the same body segment used to press the rifle trigger, might reveal some effects of the motor experience involved in the sport practice. Specifically, two comparisons seemed particularly interesting: (a) the MRCP difference between expert and nonexpert subjects, and (b) the difference between right and left finger movements. Regarding the first point, a reduced amplitude and/or latency of one or more than one MRCP component should mark the processing economy of the expert group (20). Regarding point b, the question is whether economy is a general phenomenon, nonlateralized (thus present for both left and right finger movements), or specific for the movement of the body segment most active during sport training (the right finger, which presses the rifle trigger). The latter result (the lateralization) is expected in accordance with the principles of specificity of brain adaptation (13,22), which suggests physiological adaptation to the particular overloads imposed by the training process.

MATERIALS AND METHODS

Subjects. Ten professional clay-target shooters (two females; mean age 27.7 yr) and 12 novices without any shooting experience (three females; mean age 29.1 yr) participated in the experiment; the control group was matched for age and sex with the shooters' group (all *P* values, not significant). The dominant hand and eye were assessed by a modified version of the Edinburgh inventory (29); in all cases, the right hand and eye were dominant. The professional shooters had at least 6 yr of training (mean 10 yr) in at least two of the three Olympic shotgun disciplines (trap, double trap, and skeet). They practiced shooting at least 16 h·wk⁻¹ and participated in national and international championships (e.g., the Olympic Games in 2000 and 2004). Written informed consent was obtained from all participants after the procedures, approved by the local ethical committee, had been completely explained to them.

Design. Participants made self-paced flexion movements with the index finger of their left or right hand by pressing one of two response keys alternating the left index finger response button on the first trial, the right index finger response button on the second trial, and so on (for more details about the paradigm, see Di Russo et al. (9) and Dirnberger et al. (10)).

Procedure. Participants were comfortably seated with their arms resting on a pillow placed on their laps. Two buttons (on a response pad) were placed at a distance that allowed the subjects to reach them comfortably with their index fingers. The interbutton distance was 6 cm. Subjects were instructed to rest their two fingers on the appropriate buttons. Before starting the task, and during its execution, subjects had to fixate on a point straight ahead to minimize eye movements and avoid looking directly at their hands (eye movements introduce artifacts in the EEG). Subjects made self-paced brisk flexion movements. Movements had to be fast and irregularly paced and not earlier than 5 s after the previous movement (this relatively long time interval allowed optimal segregation of neural activity related to

motion preparation). Subjects were told not to count or engage in any other rhythmic activity during the session. The subjects' average intermovement interval was 7.6 s. A block lasted until a minimum of 50 movement repetitions had been executed for each finger (maximum duration of a block was 20 min). Three blocks per finger were executed with breaks between blocks of approximately 10 min. Total time taken to complete the tasks was about 1.5 h. The total number of trials per finger was 150.

Electrophysiological recording and data analysis. The EEG was recorded from a 64-channel amplifier (Brain Products™) using part of the 10–10 system (25) electrode montage (Fp1, Fp2, AF3, AFz, AF4, F7, F3, Fz, F4, F8, FC5, FC3, FC1, FCz, FC2, FC4, FC6, T7, C5, C3, C1, Cz, C2, C4, C6, T8, M2, TP7, CP5, CP3, CP1, CP2, CP4, CP6, TP8, P7, P5, P3, P1, Pz, P2, P4, P6, P8, PO7, PO3, PO1, POz, PO2, PO4, PO8, O1, Oz, O2, I5, I3, Iz, I4, I6, SI3, SIz, and SI4). All scalp channels were referenced to the left mastoid (M1) and linked to ground by CPz. Horizontal eye movements were monitored with a bipolar recording from electrodes at the left and right outer canthi. Blinks and vertical eye movements were recorded from an electrode below the left eye, which was referenced to Fp1. The EEG from each electrode site was digitized at 250 Hz with an amplifier bandpass of 0.005 to 60 Hz together with a 50-Hz notch filter and was stored for off-line averaging. Computerized artifact rejection was performed before signal averaging in order to discard epochs in which deviations in eye position, blinks, or amplifier blocking occurred. In addition, epochs with intermovement intervals that were too short were not included in further analyses. On average, about 9% of the trials were rejected due to violation of these artifact criteria. Blinks were the most frequent cause of rejection.

For each trial, the EEG was averaged with reference to movement onset. The period used for statistical analysis started 1500 ms before movement onset, and lasted 200 ms after movement onset. The baseline for amplitude measurement was calculated from 3500 to 2500 ms before movement onset. Pulses generated by response keys (NeuroScan™ STIM pad system) served as triggers to average brain activity. To further reduce high-frequency noise, the averaged MRCP were low-pass filtered at 10 Hz. MRCP usually include BP and NS' components, whereas MP and RAP are classified as postmotor potentials according to Becker and Kristeva (4). For simplicity, in the present article, the term MRCP refers to all four components. For statistical analysis, the amplitude of each component was measured from the following electrodes contralateral to the hand where the amplitude was maximal: C3 or C4 for BP and NS', and FC1 or FC2 for MP and RAP. The BP amplitude was defined as the mean amplitude in the time window between -1500 ms and -500 ms; the BP peak was defined as the largest negativity of the initial slope; the NS' amplitude was measured between -500 ms and -50 ms minus the BP peak; the MP amplitude was measured from the NS' peak to the MP peak; the RAP amplitude was measured at the peak. We also measured the onset latency of

the BP and NS' components and the peak latency of the MP and RAP components. The BP onset latency was calculated as the time point where the signal was larger than the baseline (i.e., the mean amplitude calculated between -3500 and -2500 ms) plus the baseline standard error. The NS' onset latency corresponded to the BP peak. The amplitudes and latencies of these components were submitted to separate ANOVA with group (shooters vs controls) as unreplicated factor and finger (left vs right) as repeated measure. The Greenhouse–Geisser correction was applied to the results. Duncan *post hoc* tests were performed. The significance level was set at $P < 0.05$.

Modeling of MRCP sources. Estimation of the dipolar sources of MRCP components was carried out using the brain electrical source analysis system (BESA 2000 v. 5.0). The BESA algorithm estimates the location and the orientation of multiple equivalent dipolar sources by calculating the scalp distribution that would be obtained for a given dipole model (forward solution) and comparing it with the original MRCP distribution. Interactive changes in the location and orientation of the dipole sources led to minimization of the residual variance (RV) between the model and the observed spatiotemporal MRCP distribution (23). In these calculations, BESA made a realistic approximation of the head with the radius obtained from the average of the two groups of subjects (shooters, 89 mm; controls, 90 mm). The realistic model of the head is an improvement over the classical spherical approximation (8,33). Single dipoles were fit sequentially over specific latency ranges (given below) to correspond to the distinctive components in the waveform. Dipoles accounting for the earlier portions of the waveform were left in place as additional dipoles were added. The reported dipole fits remained consistent as a function of the starting position. A Polhemus spatial digitizer was used to record the three-dimensional coordinates of each electrode and of three fiducial landmarks (the left and right preauricular points and the nasion). A computer algorithm was used to calculate the best-fit sphere that encompassed the array of electrode sites and to determine their spherical coordinates. The mean spherical coordinates for each site averaged across all subjects were used for the topographic mapping and source localization procedures. In addition, individual spherical coordinates were related to the corresponding digitized fiducial landmarks and to the fiducial landmarks identified on the standardized finite element model (FEM) of BESA 2000. The standardized FEM was created from an averaged head using 24 individual MRI scans in Talairach space. The averaged head is used for the standard MRI displays and shows a three-dimensional brain. Major sulci can be identified. The standardized FEM provides a realistic approximation of the average head.

RESULTS

Movement-related cortical potentials. Figure 1 and 2 shows the grand average MRCP for the two groups (represented by superimposed lines). Data are reported for

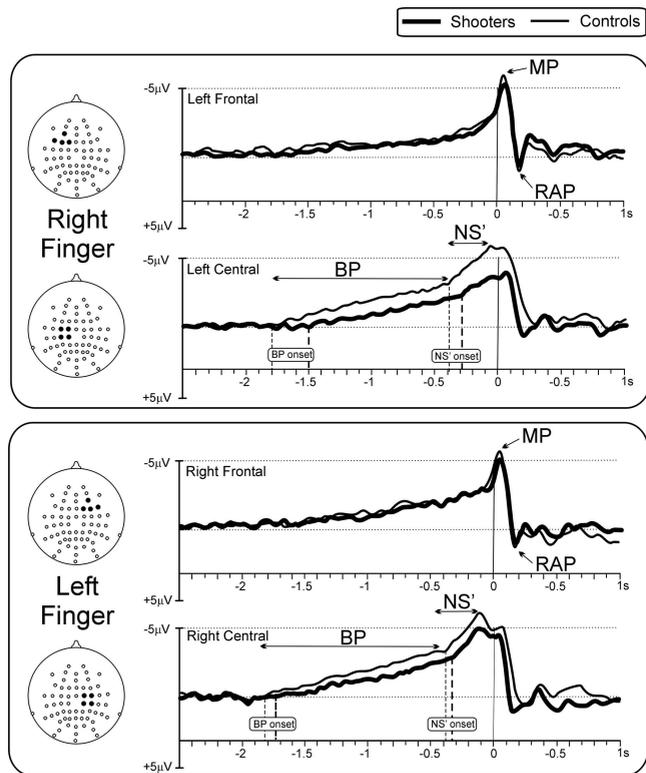


FIGURE 1—Grand average movement-related cortical potential (MRCP) for controls (blue lines) and shooters (red lines) performing flexion of the left (top) and right (bottom) index finger. The MRCP waveforms are pooled in two groups (frontal and centroparietal) of contralateral electrodes indicated in the head scheme located on the left side.

both right and left (bottom) finger movements. The waveforms shown were recorded from frontal and central pools of electrodes (filled circles on the left side of the figure). As typically reported (8), in the control group the initial gentle negativity, that is, the BP component, started rising at about 1800 ms before movement onset. The NS' component, characterized by a steeper rise, was present in the last 500

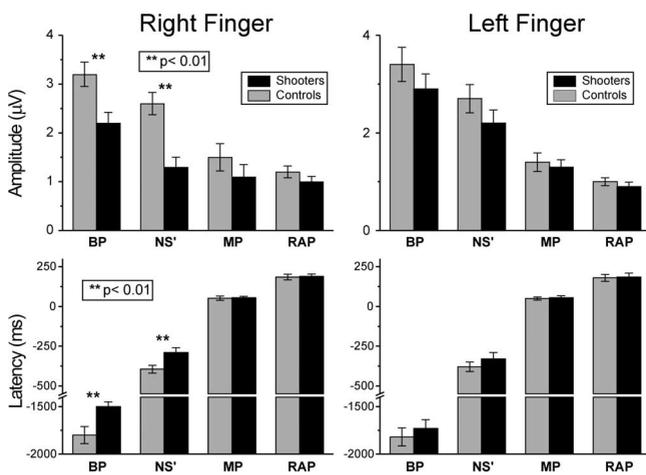


FIGURE 2—Mean amplitude (absolute values) and latency of the MRCP components over contralateral electrodes for controls (blue boxes) and shooters (red boxes), separately for movements with left and right finger. Vertical bars indicate SE. Significant differences between the two groups are indicated by stars.

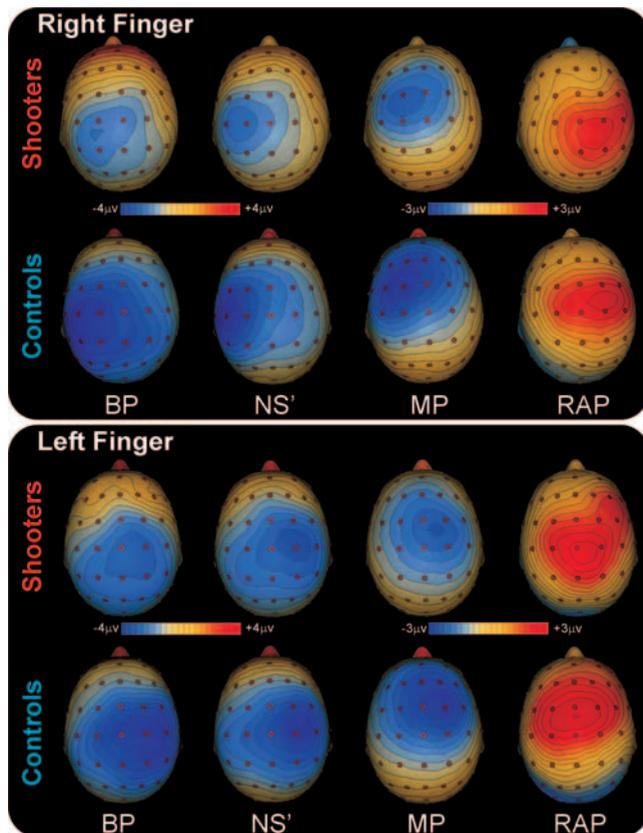


FIGURE 3—Spline-interpolated voltage maps of the MRCP components elicited by right (top) and left (bottom) finger movement. The first row of each panel shows control data and the second row shows shooter data.

ms before movement. These two components were more evident from recordings at central electrodes (see the second and fourth traces of Fig. 1). The MP component was observed around movement, peaking at 50 ms following movement (hereafter, +50 ms). The positive RAP wave peaked at about +160 ms. MP and RAP components were more evident in frontal recordings (first and third traces of Fig. 1).

The MRCP of the shooter and control groups were similar in terms of components (Fig. 1) and topography (Fig. 3). However, interesting differences between groups can be observed in Figure 1 and in statistical analyses (Fig. 2 and Table 1). In the ANOVA on BP amplitude and latency, the interaction between group and finger was significant (Table 1). Right finger movements were associated with a BP component that was smaller and started later in shooters

TABLE 1. P values of the main factors and interaction in the ANOVA analysis.

Component	Group	Finger	Interaction
Amplitude			
BP	0.041	0.038	<0.005
NS'	NS	NS	<0.010
MP	NS	NS	NS
RAP	NS	NS	NS
Latency			
BP onset	NS	NS	<0.01
NS' onset	NS	NS	<0.01
MP peak	NS	NS	NS
RAP peak	NS	NS	NS

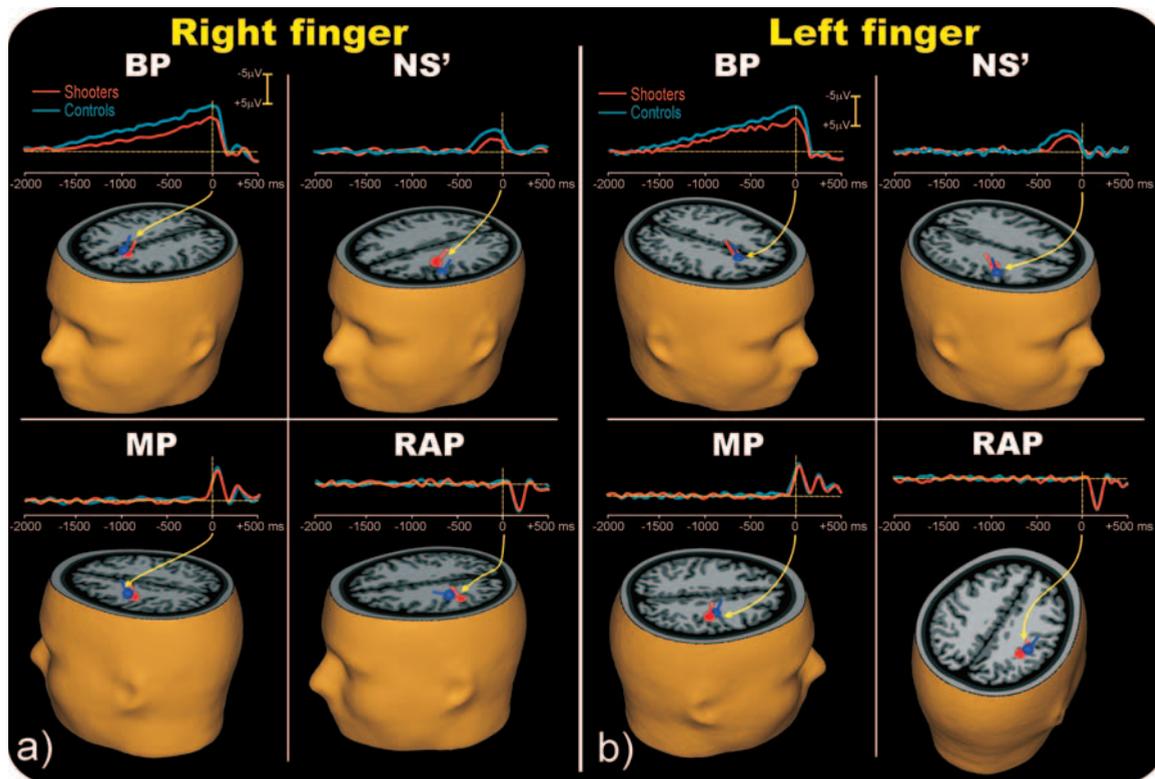


FIGURE 4—BESA dipole models fit to the grand average MRCP of controls (*blue spheres with pointer*) and shooters (*red spheres with pointers*) related to right (a) and left (b) finger movement. Modeled sources are displayed on a three-dimensional representation of the brain and in the corresponding bidimensional slices of the BESA template. Waveforms show the time course of source activity for each of the modeled dipoles (a, dipoles fitting the BP component; b, dipoles fitting the NS'; c, dipole fitting the MP; and d, dipole fitting the RAP component).

than in controls (see the waveform recorded from left central electrodes in Figure 1). *Post hoc* tests showed that for the right finger movement, the shooters' BP amplitude was smaller than that of the controls (shooters: $-2.2 \mu\text{V}$; controls: $-3.2 \mu\text{V}$; $P < 0.05$) and the amplitude of the left finger movement of both groups (shooters: $-2.9 \mu\text{V}$; controls: $-3.4 \mu\text{V}$; $P < 0.01$). For the right finger movement, BP onset was later in shooters than in controls (shooters: -1500 ms ; controls: -1800 ms ; $P < 0.001$), and later than left finger onset in both groups (shooters: -1730 ms ; controls: -1820 ms ; $P < 0.01$). No other comparisons were significant. As for BP, also the analysis of NS' amplitude and latency indicated a significant interaction between group and finger (Table 1). *Post hoc* tests showed that for the right finger, the NS' amplitude was significantly reduced in shooters (shooters: $-1.3 \mu\text{V}$; controls: $-2.6 \mu\text{V}$; $P < 0.005$) and was the smaller of the NS' for the left finger movements in both groups (shooters: $-2.2 \mu\text{V}$; controls: $-2.7 \mu\text{V}$; $P < 0.01$). For the right finger movement, the NS' onset was later in shooters than in controls (shooters: -290 ms ; controls: -395 ms ; $P < 0.01$), and later than both groups' left finger movements (shooters: -330 ms ; controls: -380 ms ; $P < 0.01$). No other comparisons were significant. As shown in Table 1, for MP and RAP components, no difference was found between groups and fingers either for amplitude (mean MP amplitude: $-1.3 \mu\text{V}$, mean RAP amplitude: $1.1 \mu\text{V}$) or latency (mean MP latency: $+54 \text{ ms}$; mean RAP latency: $+187 \text{ ms}$).

The first row of each panel in Figure 3 shows a top view of the scalp potential distribution for the left and right fingers in the -1500 to 150 ms time window. The BP showed widespread, symmetrical distribution over the centroparietal areas, whereas the NS' was contralaterally predominant over the centrofrontal areas. The MP showed focal distribution in the contralateral sensorimotor area. The RAP showed tangential activity with the positive pole centered over the frontal areas and the negative pole over the occipitoparietal areas. A qualitative comparison of the two groups' topography suggests that brain activity was more broadly distributed across the scalp in controls than in shooters, a phenomenon particularly marked in the case of right finger movement.

Source analysis. MRCP were decomposed in four time windows corresponding to the BP (-1500 – 400 ms), NS' (-400 – 50 ms), MP (0 – $+100 \text{ ms}$), and RAP ($+100$ – $+200 \text{ ms}$) components. As shown in Figure 4a and b for right and left fingers, respectively, the BP time window was fit with a dipole with a radial (to the head surface) orientation (red for shooters and blue for controls) located in the medial frontal cortex, slightly contralateral to the midline in the proximity of the SMA. The source activity, starting around -2000 ms , was quite similar to the BP component recorded on the scalp. The NS' time window was fit with a radial dipole, which was contralaterally situated in the anterior motor cortex, suggesting activity in the PMA; the source activity of this dipole peaked just before the move-

ment, as did the NS'. The MP time window was fit with a slightly tangentially oriented dipole, located in the contralateral motor cortex; the source activity, which peaked after the movement, was quite similar to the MP. The RAP time window was fit with a clearly tangential dipole with a frontal positive pole and a posterior negative pole (bipolar distribution); the resulting location was in the contralateral somatosensory cortex and the source activity was quite similar to the RAP. The residual variance of the model was 2.34% for right finger and 2.65% for left finger movements in the $-1500 +150$ time window.

Comparison of the dipole locations and the orientations of the two groups suggest that they were quite similar. However, comparison of the dipole source waveforms (dipole moment) shows large differences in terms of amplitude and onset latency of the SMA and PMA activity. In particular, as noted for the surface waveforms, brain activity occurring before the movement was reduced and delayed in shooters with respect to control subjects (compare red and blue waveforms in Fig. 4).

DISCUSSION

In top-level shooters, BP and NS' components related to right finger movements had a later onset and reduced amplitude with respect to control subjects' data. This finding confirms and extends previous data collected in kendoists (20), supporting the hypothesis that following practice, a motor task is performed at a lower metabolic cost.

Source analysis allowed us to specify the cortical areas in which economy takes place. Motor preparation required less time and less neuron recruitment in the left SMA and PMA. Economy may be due to a smaller number of SMA and PMA neurons active for movement preparation. This effect might be mediated by a reduction of synaptic connections; these would be diffuse at first and become specific by long-term potentiation through practice (2). Alternatively, the activity might involve the same neural population and be less sustained in time. The present data do not allow us to distinguish between the two not mutually exclusive hypotheses. Scalp potential distribution shows more widespread activity for novices. However, this wider distribution is compatible with the larger amplitude of BP and NS' components measured in novices and the properties of volume-conducted currents. In any case, dipole analysis allows us to conclude that the cortical generators responsible for the components associated with motor preparation (i.e., SMA and PMA) were not different in the two groups of subjects. If the shooters' movements were more automatic and required less effort (18,19), this was not mediated by a change in the cortical structures responsible for it. However, we cannot exclude that the reduction in amplitude observed in the expert athletes may be due to a greater involvement of subcortical structures not detectable by surface recordings, such as ERP (28).

In contrast to what we observed for the motor preparation phase, no difference was found between groups for MP and RAP. The lack of difference for MP indicates that the daily

shooting training did not change the activity pattern of the primary motor cortex specifying the motor commands for finger movement. A similar consideration applies to the lack of effect on RAP, the activity of the primary somatosensory cortex evoked by the sensory feedback associated with movement. This latter activity was the same in the two groups. Although the RAP component was not investigated in Kita et al. (20), these authors also found that MP was not different in athletes and control subjects. Overall, at least for a very simple task such as that used in the present study, the detectable marker of motor expertise at the cortical level is a tuning, in terms of amplitude and latency, of action preparation rather than execution.

One may think that the lack of effect on primary motor and sensory cortices and data showing higher cortical activation for a skilled function (15,16) are findings that are at odds with each other. This position should be taken cautiously, however, if one also considers that we are far from knowing the relation between phenomena observed at the electrophysiological level and the oxygen-consumption level. fMRI technique collects data that are integrated across long period of time, not distinguishing between different brain events; in contrast, event-related potentials describe the chronometry of brain activity, and different wave components are associated with distinct brain events. Moreover, the two techniques imply important variations of the experimental paradigms (e.g., single movement vs movement sequence). Overall, it is not surprising that the available data do not yet offer a unitary vision, despite the recognition that each one contributes to the general understanding.

Particularly interesting is the comparison between left and right finger data. The group difference for the BP and NS' components was present only when the athletes performed with their right finger, that is, the finger used for pressing the rifle trigger when shooting. As stated in the introduction, one of the differences in the brain activity of expert and naïve subjects performing a motor task is the lateralized pattern of results. For shooters, this lateralization effect resulted in left hemispheric specialization (i.e., shorter motor preparation only for the right hand). This finding supports the view that the effects observed on cortical activity related to motor preparation in shooters is due to the specific sport practice. If it reflects general higher ability of "motor readiness" in athletes with respect to novices, it should also be present for the left finger movement. Overall, sport experience seems to facilitate planning and selection of a specific movement.

The present findings of motor expertise affecting laterality profile (and, specifically, increasing left hemisphere dominance) do not generalize to other motor skills. For instance, Mikheev et al. (24) showed enhanced right hemispheric specialization in highly qualified judo wrestlers. With respect to wrestling, shooting involves a lower degree of bimanual coordination, and is more linked to dexterity of hand and forearm (at least for right hand- and right eye-dominant athletes, such as in the present group). Because these aspects are strongly controlled by the left hemisphere, overtraining of motor skills was expected to be associated

with major left rather than right hemisphere involvement (see Haaland et al. (12) for a review).

It should be noted that we are dealing with hyperlearning of an *elementary* motor act. To press a key is a simple task for everyone. The movement tested involved the same body segment used for pressing the trigger of the rifle, but the action was extracted from a complex sport-specific sequence, that is, calling for a target, holding the rifle, aiming, and pressing the trigger. One might have expected that the elementary level of the task would have canceled the athletes' advantage. In contrast, the difference between groups was clear. Thus, additional motor experience, such as that involved in daily sport training, may represent a hyperlearning experience that modifies the pattern of brain activity coding for motor preparation of a very simple action.

The present findings on hand movements are consistent with previous results on eye movements in a similar group of top-level shooters (9). Shooters showed an advantage with respect to control subjects in the simple task of saccades toward a visual target. Their saccadic reaction time was reduced with respect to controls. In light of the present results, we can interpret this advantage in terms of shorter saccadic motor preparation consequent to hyperlearning of eye movements following the training involved in shooting

practice. The biological significance of the present findings is open to speculation. However, data are compatible with the general principle that motor exercise involved in sport increases psychomotor efficiency. According to Hatfield and Hillman (13), efficiency is defined as the ratio between psychomotor behavior and neural resource allocation. Efficient resource allocation may reduce the strain on the organism (30). For shooters, the challenge is precise timing and visuospatially coordinated action during practice of the triggering action. The present data show that shooting experience is associated with reduced neural activity in motor preparation, suggesting a more refined neural organization of this process.

At different levels, the general rule of specificity of adaptation and economy was already shown for athletes. For instance, specific metabolic adaptations occur in the muscles recruited for the specific sport (22); a decrement in motor activity recruitment was measured by integrated EMG activity following resistance training (7). The present findings indicate that the same rule is valid for the CNS at the level of motor programming.

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REFERENCES

1. ABERNETHY, B., and R. J. NEAL. Visual characteristics of clay target shooters. *J.Sci. Med. Sport* 2:1–19, 1999.
2. ASANUMA, H., and C. PAVLIDES. Neurobiological basis of motor learning in mammals. *Neuroreport* 8:i–vi, 1997.
3. BARALDI, P., C. A. PORRO, M. SERAFINI, et al. Bilateral representation of sequential finger movements in human cortical areas. *Neurosci. Lett.* 2:95–98, 1999.
4. BECKER, W. and R. KRISTEVA. Cerebral potentials prior to various force deployments. *Prog. Brain Res.* 54:189–194, 1980.
5. CREWS, D. J., and D. M. LANDERS. EEG measures of attentional patterns prior to golf putt. *Med. Sci. Sports Exerc.* 25:116–126, 1993.
6. DEECKE, L. P. H. SCHEID, and H. KORNHUBER. Further studies on human cerebral potentials preceding voluntary movements. *Exp. Brain Res.* 7:158–168, 1969.
7. DE VRIES, H. A. Efficiency of electrical activity as a physiological measure of the functional state of the muscle tissue. *Am. J. Phys. Med.* 47:10–22, 1968.
8. DI RUSSO, F., C. INCOCCIA, R. FORMISANO, U. SABATINI, and P. ZOCOLOTTI. Abnormal motor preparation in severe traumatic brain injury with good recovery. *J. Neurotrauma* 22:297–312, 2005.
9. DI RUSSO, F., S. PITZALIS, and D. SPINELLI. Fixation stability and saccadic latency in elite shooters. *Vis. Res.* 43:1837–1845, 2003.
10. DIRNBERGER, G., M. REUMANN, W. ENDL, G. LINDINGER, W. LANG, and J. ROTHWELL. Dissociation of motor preparation from memory and attentional processes using movement-related cortical potentials. *Exp. Brain Res.* 135:231–240, 2000.
11. ELBERT, T., C. PANTEV, C. WIENBRUCH, B. ROCKSTROH, and E. TAUB. Increased cortical representation of the fingers of the left hand string players. *Science* 270:305–307, 1995.
12. HAALAND, K. Y., C. L. ELSINGER, A. R. MAYER, S. DURGERIAN, and S. M. RAO. Motor sequence complexity and performing hand produce differential patterns of hemispheric lateralization. *J. Cogn. Neurosci.* 4:621–636, 2004.
13. Hatfield, B. D., and Hillman. C. H. The psychology of sport: a mechanistic understanding of the psychology of superior performance. In: *Handbook of Sport Psychology*, Singer, R. N. Hausenblas, and H. A. Janelle C. M. (Eds.) New York: John Wiley & Sons, 2001, pp. 362–386.
14. HAUFLE, A. J. T. W. SPALDING, D. L. SANTA MARIA, and B. D. HATFIELD. Neuro-cognitive activity during self-paced visuospatial task: comparative EEG profiles in marksmen and novice shooters. *Biol. Psychol.* 53:131–160, 2000.
15. KARNI, A., G. MEYER, P. JEZZARD, M. M. ADAMS, R. TURNER, and L. G. UNGERLEIDER. Functional MRI evidence for adult motor cortex plasticity during motor skill learning. *Nature* 377:155–158, 1995.
16. KARNI, A., G. MEYER, C. REY HIPOLITO, P. JEZZARD, M. M. ADAMS, R. TURNER, and L. G. UNGERLEIDER. The acquisition of skilled motor performance: fast and slow experience-driven changes in primary motor cortex. *Proc. Natl. Acad. Sci. U S A.* 95:861–868, 1998.
17. KAWASHIMA, R., K. YAMADA, S. KINOMURA, et al. Regional cerebral blood flow changes of cortical motor areas and prefrontal areas in humans related to ipsilateral and contralateral hand movement. *Brain Res.* 1:33–40, 1993.
18. KERICK, S. E., L. W. DOUGLASS, and B. D. HATFIELD. Cerebral cortical adaptations associated with visuomotor practice. *Med. Sci. Sports Exerc.* 36:118–129, 2004.
19. KERICK, S. E., K. McDOWELL, T. M. HUNG, D. L. SANTA MARIA, T. W. SPALDING, and B. D. HATFIELD. The role of the left temporal region under the cognitive motor demands of shooting in skilled marksmen. *Biol. Psychol.* 58:263–277, 2001.
20. KITA, Y., A. MORI, and M. NARA. Two types of movement-related cortical potentials preceding wrist extension in humans. *Neuroreport* 12:2221–2225, 2001.
21. KRINGS, T. R. and TOPPER. Cortical activation patterns during complex motor tasks in piano players and control subjects. A functional magnetic resonance imaging study. *Neurosci. Lett.* 278: 189–193, 2000.
22. MCARDLE, W. D., F. I. KATCH, and V. L. KATCH. *Exercise Physiology: Energy, Nutrition, and Human Performance*. Philadelphia: Lea & Febiger, 1986.
23. MILTNER, W., C. BRAUN, R. J. JOHNSON, G. V. SIMPSON, and D. S. RUCHKIN. A test of brain electrical source analysis (BESA): a simulation study. *Electroencephalogr. Clin. Neurophysiol.* 91:295–310, 1994.
24. MIKHEEV, M., C. MOHR, S. AFANASIEV, T. LANDIS, and G. THUT.

- Motor control and cerebral hemispheric specialization in highly qualified judo wrestlers. *Neuropsychologia* 8:1209–1219, 2002.
25. NUWER, M. R., F. L. LEHMANN, D. DA SILVA, S. MATSUOKA, W. SUTHERLING, and J. F. VIBERT. IFCN guidelines for topographic and frequency analysis of EEGs and EPs. The International Federation of Clinical Neurophysiology. *Electroencephalogr. Clin. Neurophysiol. Suppl.* 52:15–20, 1999.
 26. PASCUAL-LEONE, A., E. M. WASSERMAN, N. SADATO, and M. HALLETT. The role of reading activity on the modulation of motor cortical outputs to the reading hand in Braille readers. *Ann. Neurol.* 38:910–915, 1995.
 27. PETRUZZELLO, S. J. and D. M. LANDERS. State anxiety reduction and exercise: does hemispheric activation reflect such changes? *Med. Sci. Sports Exerc.* 8:1028–1035, 1994.
 28. REKTOR, I. Scalp-recorded Bereitschaftspotential is the result of the activity of cortical and subcortical generators: a hypothesis. *Clin. Neurophysiol.* 12:1998–2005, 2002.
 29. SALMASO, D., A. M. and LONGONI. Problems in the assessment of hand preference. *Cortex* 4:533–549, 1985.
 30. SELYE, H. *The Stress of Life*. New York: McGraw-Hill, 1976.
 31. SHAW, J. C. Electroencephalographic measures of attentional patterns prior to golf putt. *Med. Sci. Sports Exerc.* 9:1084–1085, 1993.
 32. TARKKA, I. M. Electrical source localization of human movement-related cortical potentials. *Int. J. Psychophysiol.* 16:81–88, 1994.
 33. TOMA, K., T. MATSUOKA, and I. IMMISCH. Generators of movement-related cortical potentials: fMRI-constrained EEG dipole source analysis. *Neuroimage* 17:161–173, 2002.